THE EVOLUTION OF THE VASCULAR TISSUE OF PLANTS.

W. C. WORSDELL.

(WITH SEVEN FIGURES)

IT is a sign of the times and of the natural progress which botanical science is making that the evolution of the more deeply seated part of the organization of plants is beginning to receive attention. The most vital and important part of the anatomical structure is doubtless that of the vascular system, and it is the development of this upward through some of the most important groups of plants of which I propose to take a general survey.

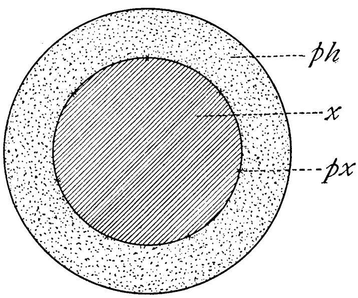

FIG. 1.—The protostele: *x*, xylem; *px*, protoxylem; *ph*, phloem.

We appear to be justified in looking for the primary origin of the complex vascular structure of the stems of cormophytes in the single *solid stele*, the *protostele*, consisting of a central mass of wood, or xylem, surrounded by a zone of bast, or phloem (*fig 1*), this in its turn having been derived from the primitive conductive tissue of the sporophytic stem of some bryophytic ancestor. If we take the great group of the ferns this structure always appears as the first stage in the individual development of each type, as has been shown by the researches of Leclerc du Sablon[1] and others. This is also the type found in the mature vascular structure of several of the most primitive ferns, such as the Hymenophyllaceae, Lygodium (Schizaeaceae), and Gleichenia, among modern forms, and Botryopteris among fossils.

[1] SABLON, LECLERC DU, Recherches sur la Tige des Fougères. Ann. Sci. Nat. Bot. VII. 11 : —. 1890.

The next stage in general evolution, as the writer holds, is that in which a *pith arises in the center of the solid stele* (*fig. 2.*), on the outer limit of which an endodermis, or starch-sheath, may or may not be present; this is seen in such forms as Platyzoma (Gleicheniaceae,) Schizaea, the Ophioglossaceae, and in the fossils Zygopteris and Anachoropteris (Botryopterideae). The possibility, however, of these forms having been *reduced* from type 3 is not excluded. In all these ferns the protoxylem, or first-formed portion of the wood, is either situated within the metaxylem, or later-formed portion, a short distance from the periphery, or else, as in Lygodium, quite at the periphery; that is to say, the xylem is chiefly *centripetal* in its development.

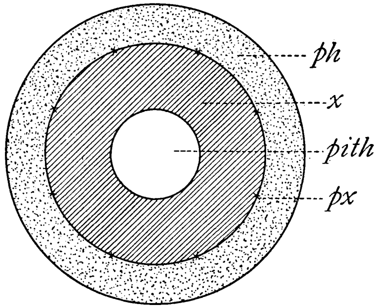

FIG. 2.—The tubular stele with central pith: *x*, *px*, *ph*, as in *fig. 1.*

The *solenostele* is the name given to the third stage of differentiation, in which to the internal endodermis is added an *internal zone of phloem* (*fig. 3.*); this is found in Matonia, Loxsoma, *Aneimia Mexicana* (Schizaeaceae), and in a few other plants, such as *Medullosa stellata* among the Cycadofilices.

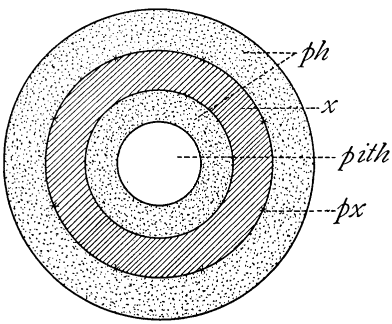

FIG. 3.—The solenostele: reference letters as before.

The *dialystelic* condition appears to have been the next step onward, in which the tubular solenostele becomes split up into a number of secondary solid steles or *concentric* strands (*fig. 4*), the protoxylem, as in the previous stages, being situated at or near the external limits of the xylem. This structure is directly due to the crowded arrangement of the leaves on the stem, so that frequent gaps in the original solenostele become inevitable in order to allow of the passing out of the leaf-trace

bundles; the whole is thus merely a variant on the solenostele, in which latter the leaf-insertions are not crowded; both conditions belong essentially, as Jeffrey[2] has admirably shown, to the *siphonostelic*, or tubular type of stele. Van Tieghem[3] was therefore in error in regarding the dialystelic condition as derived merely from branching of the primitive solid stele. Dialystely is very common in ferns, occurring in Marattiaceae, *Aneimia Phyllitidis* (Schizaeaceae), Cyatheaceae, Dicksoniae, and in almost all Polypodiaceae, the most advanced of the fern series. The vascular cylinders of *Osmunda regalis* and *O. cinnamomea* probably represent, as Jeffrey[4] has recently suggested, *reduced* forms, in a greater and a less degree respectively, of the dialystelic condition. It is also found in several of the Cycadofilices, the group intermediate between ferns and cycads, such as the Medulloseae and Cladoxylon, all fossil types.

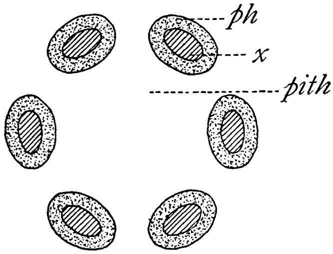

FIG. 4.— The dialystelic condition.

If we now take these last named *polystelic* plants as our starting point, we may trace from them the origin and evolution of the vascular tissue of the gymnosperms. The modification which eventually produced this latter consisted, as the writer, along with Potonié,[5] holds, in the gradual reduction of the concentric type of bundle or stele to form the first and simplest *collateral* type. In a form like *Medullosa anglica* there is a single ring of concentric steles. The theory which the writer regards as best explaining the facts is this: in order that it might give rise to the next succeeding type, as he regards it, represented by such forms as the fossil Cycadofilices, *Lyginodendron Old-*

[2] JEFFREY, E. C., Trans. Brit. Assoc. Adv. Sci. 869. 1897; Mem. Bost. Soc. Nat. Hist. V. 5: 160.

[3] VAN TIEGHEM, PH., Sur la Polystélie. Ann. Sci. Nat. Bot. VII. 3: —. 1886; Traité de Botanique, p. 1370. 1892.

[4] JEFFREY, E. C., The structure and development of the stem in pteridophytes and gymnosperms. Phil. Trans. Roy. Soc. June 1902.

[5] POTONIÉ, Lehrbuch Pflanzenpalaeontologie, 1899.

hamium, Poroxylon, and others, each concentric stele composing the cylinder of Medullosa underwent a reduction of the tissue on its inner side, whereby the phloem and the whole of the secondary wood of that side vanished, leaving behind what is known as a *mesarch* bundle, consisting of a central or an external protoxylem, with a group of primary metaxylem on both its inner and outer side, or solely in the former region; as a rule, a greater or less development of secondary wood and phloem occurs on the outer side of each bundle. The secondary wood usually extends across the gaps separating the bundles, toform a continuous solid cylinder enclosing a pith, thus tending eminently to obscure the original and primitive condition of a ring of reduced concentric strands (*fig.* 5). That these latter are each of them really a vestige of a concentric bundle, such as that of Medullosa, is shown very well in the case of *Lyginodendron Oldhamium* by the arc- or horseshoe-shaped outline of the bundles, as also by the occasional occurrence of secondary xylem and phloem on the *inner* side of some of the bundles, exhibiting an *inverted orientation*, as if to remind us that the concentric is the original type of structure of these strands. Dr. D. H. Scott[6] supposes that the stem cylinder of Lyginodendron has been derived from the single solid stele of Heterangium (another of the Cycadofilices from the Coal-measures), by means of the extinction of the whole of its central solid xylem with the exception of the primary tracheides on the immediate inner side of each protoxylem group. But the writer fails to see much ground for holding this view. The very compact stele of Heterangium, with the neatly and evenly circular outline of the inner limits

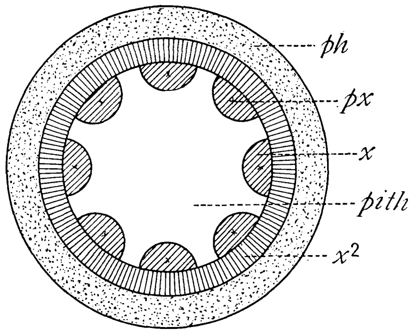

FIG. 5.—The primitive mesarch type: reference letters as before; x^2, secondary xylem.

[6] SCOTT, D. H., Studies in fossil botany, p. 340, 1900.

of the secondary wood, exhibits no sign whatever of having given rise to the more or less distinctly individualized curved bundles of the cylinder of *Lyginodendron Oldhamium.* The writer, on the contrary, believes it to be the homologue of a single stele of Medullosa, and can trace a gradual reduction in the number of steles in these plants, from the very numerous ones of *Medullosa Solmsii,* firstly, to the very few steles (two or three in number) of *M. anglica* or Colpoxylon, and finally, to the single large stele of Heterangium or of Megaloxylon. He may add, moreover, that the derivation of the tubular from the solid stele is to be sought for, not in these semi-gymnospermous forms, but much farther back, viz., among the ferns.

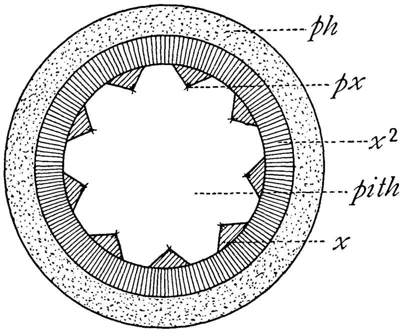

FIG. 6.—The endarch type: reference letters as before.

When we arrive at the stage of our modern cycads, which are certainly descended from some of these cycadofilicinean plants, a further modification meets our eyes, for here we find the mesarch bundle of the stem cylinder almost entirely replaced by the *endarch* type, in which the innermost primary or centripetal group of xylem has vanished, so that the protoxylem which, once upon a time in the ancient concentric bundle, occupied the center of the latter, now constitutes the most internal portion of the bundle, viz., that nearest the pith (*fig. 6*). But the older mesarch bundle has not become completely extinct throughout the group, for in that most primitive of axial organs, the peduncle of the cone, the centripetal xylem in part persists, as can be well seen in Stangeria and Bowenia. Those cycads, such as Cycas, Encephalartos, Macrozamia, and Bowenia, which possess more than one vascular cylinder in the stem, one within another to the number sometimes of a dozen (a truly striking character), are descended from such types as those Medulloseae having more than one cylinder or ring of concentric bundles,

as has been practically proved by the occurrence of obvious vestiges of the concentric type of structure, such as prevails among the Medulloseae, both in the vegetative stems and in the peduncles of all the pluricylindric forms of modern cycads.

In the Coniferae, from the yew tribe upward to the pines, as also in the Gnetaceae, all trace of the primitive mesarch type of bundle has disappeared from the stem, and we find the endarch type, with protoxylem impinging directly on the pith, universally prevailing. That ancient Devonian and Carboniferous plant, Cordaites, and our modern maidenhair tree, *Ginkgo biloba*, assumed also, in accordance probably with the exigencies of their arboreal habit, the endarch type of bundles in the stem. But *Pitys antiqua*, *P. primaeva*, *Calamopitys fascicularis*, *C. beinertiana*, and *Dadoxylon Spenceri*, forms perhaps allied to Cordaites, still retain the older mesarch type.[7]

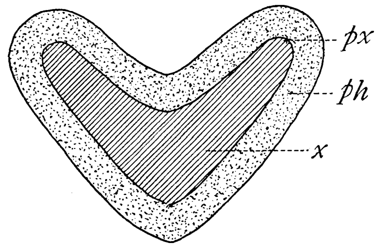

FIG. 7.— Concentric bundle of leaf-stalks.

As regards the foliar organs of all of these plants we have been considering, it is found that the primitive character of the vascular structure is in them much more persistent than it is in the stem. The concentric fern-type of bundle is still present in the leaf-stalks of Lyginodendron (Rachiopteris) and Heterangium, that of the former plant consisting of a solid stele with three or more protoxylem groups at its periphery, the whole being surrounded by phloem (*fig. 7*). In Medullosa, Cordaites, and modern cycads the bundles of the leaves are collateral and mesarch in structure; as are also those of the foliage leaves of conifers, although here the centripetal primary xylem is either greatly reduced or modified to form a quasi-new structure, the *transfusion tissue*. In Ginkgo this reduction also obtains in the foliage leaf. But in the most primitive vegetative foliar organs of the plant, the cotyledons, both in Ginkgo and Cephalotaxus (the

[7] SCOTT, D. H., On the primary structure of certain palaeozoic stems with the Dadoxylon type of wood. Trans. Roy. Soc. Edinburgh **40**: [pt. II]. 1902.

most ancient of the conifer group), the mesarch structure of the bundle is as pronounced and well developed as it is in the case of the cycads or Medulloseae. As regards these two latter groups, the writer regards their mesarch bundles as derived from the splitting up of one or more concentric bundles like that of Lyginodendron. In any case the mesarch collateral bundles of the foliar organs of all these plants are to be regarded, like those of the stem, as reductions from the concentric type. But this concentric type actually occurs here and there in the sporophylls of the cycads.

On arriving at the level of the angiospermous plants, all trace of any vestige of the old concentric type of bundle in the form of a mesarch structure has completely vanished both in the stem and in the leaf, the purely endarch structure prevailing everywhere. The faet of this type of structure occurring well-nigh universally in these plants which, in other parts of their organization, are seen to be the most advanced in evolution of all plants, is an indication that this type of vascular structure is also to be regarded as the most advanced, because the most advantageous and the best adapted to the requirements of the plants exhibiting it. The writer, however, considers that the conclusions drawn by Jeffrey, from the study of the vascular cryptogams, as to the origin of the vascular tissue of the stem are rather too hastily applied to the case of the angiosperms. We are not yet in a position to say whence the vascular system of these latter plants was derived. All we dare surmise is that, looking far enough back, it is probable that the vascular tissue of the angiosperms had an origin similar to that of the forms below them in the scale.

The cause of the disappearance of the primitive mesarch structure can be seen in tracing the evolution of the vascular tissue from such forms as the Medulloseae upward. Obviously, the most economical method of increasing the amount of vascular tissue for purposes both of conduction of water and food substances and of resistance to bending strains would be by the addition, through the means of a cambium, of new tissue on the *outer circumference* of the stele or cylinder; now, in pro-

portion as the tissue in this region increased in thickness, there took place, correlatively therewith (what, indeed, would be, *a priori*, obviously expected) a gradual reduction of the centripetal vascular tissue, viz., that on the medullary side of the protoxylem, whether secondary or primary. This can be seen beautifully exhibited within the Medulloseae group itself, eventually culminating in the stem structure of modern cycads. The process of elimination of the centripetal xylem proceeded apace, until finally the endarch stem structure of Cycads, Coniferae, Cordaites, Gnetaceae, and Dicotyledons, as being by far the most economical and advantageous method of vascular formation, eventually prevailed.

In the case of leaves there has not been such a demand for modification of the vascular tissues as was the case with the stem, hence the longer persistence of the older character in these organs.

In roots the primitive centripetal structure of the wood has been far more persistent, probably for the purpose of enabling these organs to resist central tension strains.

In Monocotyledons, although true secondary thickening does not occur, the endarch type of bundle nevertheless obtains; where the concentric structure is found, as in those cases of bundles with a central phloem, this is merely to be regarded as a modification of the endarch type.

KEW, SURREY, ENGLAND.